How the number of hinge teeth may induce errors in the taxonomy of Nuculidae and Nuculanidae (Bivalvia)

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ABSTRACT

The hinge figures as an important feature in the taxonomy of bivalves, especially when soft parts are not available. For the Protobranchia, in addition to other shell features, the number of hinge teeth is often used in taxonomic studies. However, despite the importance of the number of hinge teeth, this character is not informative when shell size measurements are not available, since the number of teeth can increase during ontogeny. In addition, intraspecific variation may be observed for the same shell-size class. Since this variation has been up to now only empirically observed, the present study provides a statistical approach to the problem by computing the linear regression between number of teeth and shell size in 310 valves from five protobranch species (family Nuculidae: *Pronucula benguelana*; *Nucula semiornata*; *Ennucula puelcha*; and family Nuculanidae: *Adrana electa*; *A. patagonica*.) All species showed a statistically significant relationship (P value < 0.0001) between these characters.

Additional Keywords: Linear regression, shell morphology, Nuculoidea, Nuculanoidea, Protobranchia, taxonomy

INTRODUCTION

The protobranchs are a dominant bivalve group at abyssal depths, encompassing a high percentage of the bivalve species found in the deep-sea (Sanders and Allen, 1973). The recent sampling of deep-sea benthic fauna and the efforts of many investigators (e.g. Allen and Sanders, 1973, 1996; Moore, 1977; Rhind and Allen, 1992; Kilburn, 1994, 1999; Gofas and Salas, 1996; Roy et al., 2000; Allen, 2008; La Perna, 2008) have increased the number of known species and enlarged the known ranges of many protobranchs, providing a source for different proposals of classification for the group (e.g. Poel, 1955; Purchon, 1959; Cox, 1960; McAlester, 1964; Newell, 1969; Verril and Bush, 1897; Yonge, 1959; Sanders and Allen, 1973; Scarlato and Starobogatov, 1985; Allen and Hannah, 1986; Maxwell, 1988; Morton, 1996; Salvini-Plawen and Steiner, 1996; Coan, Scott, and Bernard, 2000; Schneider, 2001; Giribet and Wheeler, 2002; Giribet, 2008).

Among the protobranchs, the Nuculoidea Gray, 1824, and Nuculanoidea Adams and Adams, 1858, have had a problematic taxonomic history, often with obscure rearrangements of species and unclear changes in the higher-level taxonomy of many names (for more details see Schenck, 1934; Poel, 1955; Allen and Hannah, 1986; Maxwell, 1988; Rhind and Allen, 1992; Zardus, 2002). Most of the difficulties involved in the classification of the group arise from the conservative nature of the shell shape (Allen and Hannah, 1986) and from the morphological approach, which often considers only a single set of features (Sanders and Allen, 1973).

Although several characters have been taken into account (e.g., general outline, ornamentation and microstructure of the shell), in most taxonomic descriptions of protobranchs the hinge usually is an important taxonomic feature, especially when the studied specimens lack soft parts. The shape, number, position, and spacing of the teeth are often used in the diagnoses of species and even genera (Dall, 1886; Gofas and Salas, 1996). Moreover, the differences between the number of anterior and posterior teeth are used in identification, and even differences in the order of two or three teeth have been considered significant in descriptions or identification works (e.g. Esteves, 1984; Smith, 1885; Abbott, 1974; Kilburn, 1994; Rios, 1994; Espinosa and Ortea, 2001).

However, to consider the number of teeth without associating the character to measurements of shell size is not informative, and may cause taxonomic confusion. A morphometrical approach may improve on the traditional taxonomic methods and has been used with success by several authors (Bonfitto and Sabelli, 1995; Gofas and Salas, 1996; Fuiman et al., 1999).

This paper discusses the taxonomic importance of the size of the shell in proportion to the number of teeth on the hinge in three species of Nuculidae: *Pronucula benguelana* Clarke, 1961; *Nucula semiornata* d'Orbigny,

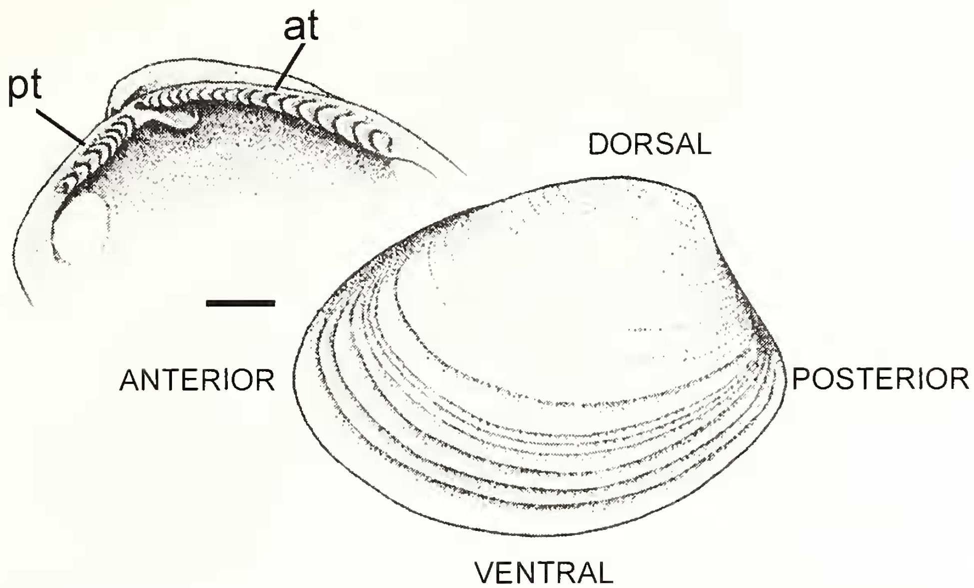


Figure 1. *Ennucula puelcha* d'Orbigny, 1842. Shell and the anterior and posterior hinge teeth. Abbreviations: at = anterior teeth; pt = posterior teeth. Seale bar = 2 mm. Adapted from Absalão & Pimenta (2005).

1846; *Ennucula puelcha* d'Orbigny, 1842; and two of Nuculanidae: *Adrana electa* (A. Adams, 1846); and *Adrana patagonica* (d'Orbigny, 1846).

MATERIALS AND METHODS

The material examined includes samples taken during different cruises undertaken the South Atlantic Ocean.

The measurements used herein are commonly used in morphometric studies with bivalves (Sibaja and Vilalobos, 1986; Bonfitto and Sabelli, 1995; Gofas and Salas, 1996; Fuiman et al., 1999), and are represented in Figure 1. The numbers of anterior and posterior teeth were counted with the aid of a ZEISS SV-6 stereoscopic microscope. The antero-posterior and dorso-ventral axes of each valve were measured using a caliper of 0.05 mm accuracy. A total of 200 valves of nuculids and 110 valves of nuculanids were considered in this study (Table 1). The statistical approach consisted of linear regression analysis (Sokal and Rohlf, 1981). All material from this study is deposited in the Mollusca collection of the Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (IBUFRJ).

Table 1. Deseriptive statistics of the material analyzed. Abbreviation: sd = Standard deviation.

Speeies names	Antero-posterior axis	Dorso-ventral axis	Anterior teeth	Posterior teeth
Pronucula benguelana (N = 23)				
Range	1.7–3.8mm	1.6–3.45mm	5–10	3–7
Mean	2.81	2.62	7.65	5.52
sd	0.55	0.50	1.27	1.20
Nucula semiornata (N = 82)				
Range	0.85–6.85mm	1.0–6.8mm	6–23	2–10
Mean	3.60	3.43	13.93	5.76
Sd	1.72	1.71	4.70	2.09
Ennucula puelcha (N = 95)				
Range	1.65–15.25mm	1.55–13.65mm	4–22	2–9
Mean	6.71	6.20	13.24	5.25
sd	3.73	3.42	4.75	1.86
Adrana electa (N = 55)				
Range	12.45–56–60mm	3.20–14.55mm	32–64	31–71
Mean	35.68	9.15	50.76	55.47
Sd	9.20	2.66	7.11	10.02
Adrana patagonica (N = 55)				
Range	5–33.3mm	1.9–9mm	16–55	19–52
Mean	17.39	5.37	31.40	33.98
sd	6.22	1.88	6.68	5.91

Table 2. Results of statistical analyses. Abbreviations: ap = antero-posterior axis; dv = dorso-ventral axis; at = anterior teeth; pt = posterior teeth.

Species names	x(ap) - y(at)	x(ap) - y(pt)	x(dv) - y(at)	x(dv) - y(pt)
P. benguelana	y = 1.798x + 2.597 R^2 = 0.607 F = 32.44 P value < 0.0001	Y = 1.68x + 0.793 R^2 = 0.589 F = 30.10 P value < 0.0001	y = 1.848x + 2.810 R^2 = 0.538 F = 24.49 P value < 0.0001	Y = 1.742x + 0.959 R^2 = 0.530 F = 23.72 P value < 0.0001
N. semiornata	y = 2.550x + 4.757 R^2 = 0.8707 F = 538.9 P value < 0.0001	Y = 1.139x + 1.659 R^2 = 0.8811 F = 592.7 P value < 0.0001	y = 2.555x + 5.152 R^2 = 0.8635 F = 506.1 P value < 0.0001	Y = 1.139x + 1.845 R^2 = 0.8693 F = 532.0 P value < 0.0001
E. puelcha	y = 1.152x + 5.514 R^2 = 0.8183 F = 418.8 P value < 0.0001	Y = 0.4425x + 2.284 R^2 = 0.7892 F = 348.1 P value < 0.0001	y = 1.266x + 5.396 R^2 = 0.8338 F = 466.5 P value < 0.0001	Y = 0.4858x + 2.241 R^2 = 0.8031 F = 379.3 P value < 0.0001
A. electa	y = 0.6188x + 28.68 R^2 = 0.6412 F = 94.73 P value < 0.0001	Y = 0.9373x + 22.03 R^2 = 0.7418 F = 152.3 P value < 0.0001	y = 1.953x + 32.90 R^2 = 0.5324 F = 60.34 P value < 0.0001	Y = 3.093x + 27.19 R^2 = 0.6732 F = 109.2 P value < 0.0001
A. patagonica	y = 1.006x + 13.90 R^2 = 0.8776 F = 380.1 P value < 0.0001	Y = 0.8626x + 18.98 R^2 = 0.8228 F = 246.1 P value < 0.0001	y = 3.205x + 14.18 R^2 = 0.8115 F = 228.2 P value < 0.0001	Y = 2.685x + 19.56 R^2 = 0.7261 F = 140.5 P value < 0.0001

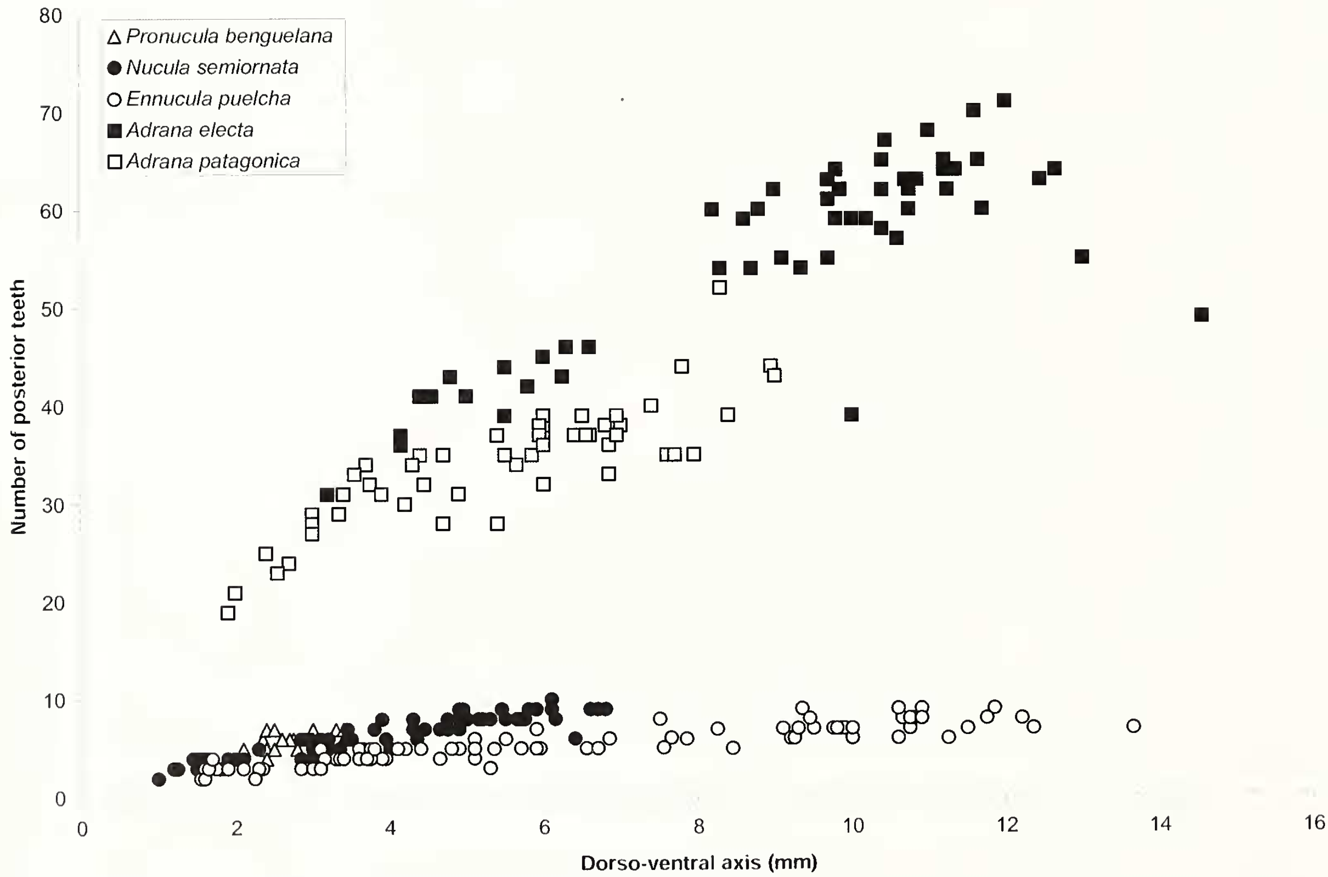
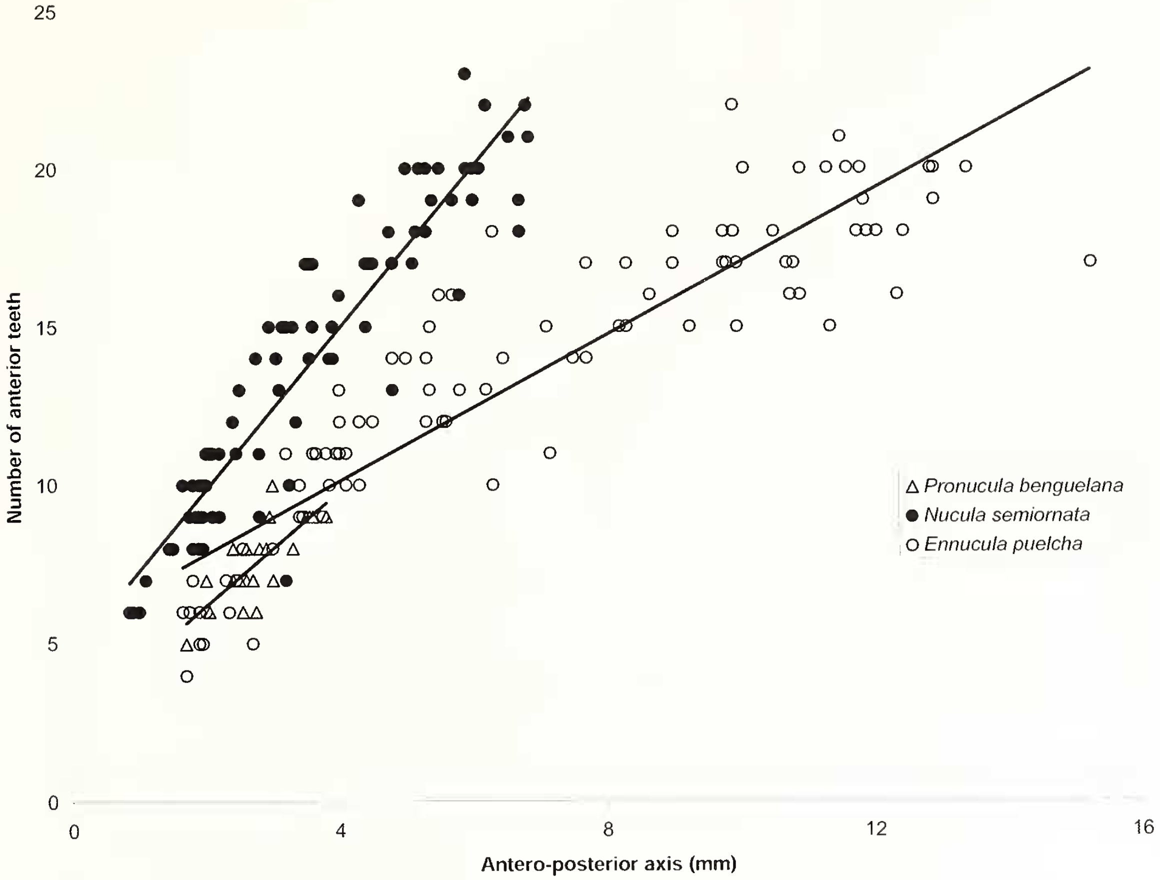


Figure 2. Relationship of dorso-ventral axis and number of posterior teeth in studied protobranch species. The two families analyzed occupy discrete morphospaces, reinforcing the importance of the number of teeth as a character at supra-specific levels.



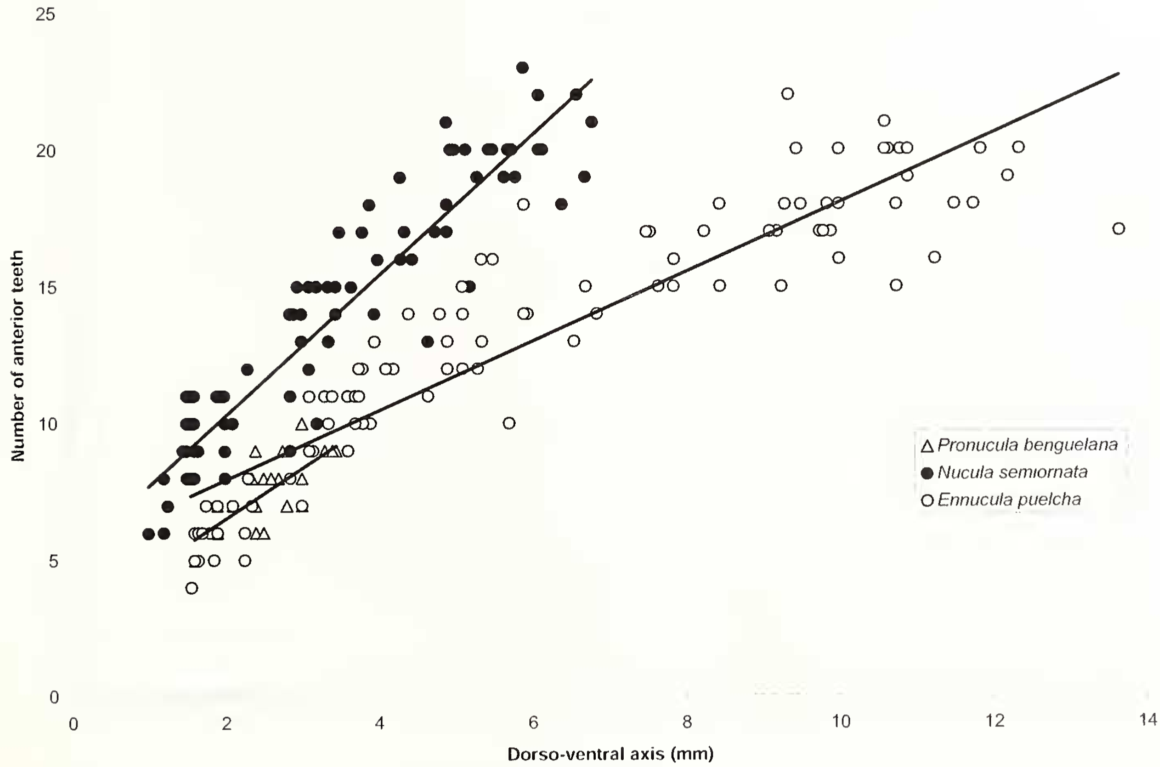
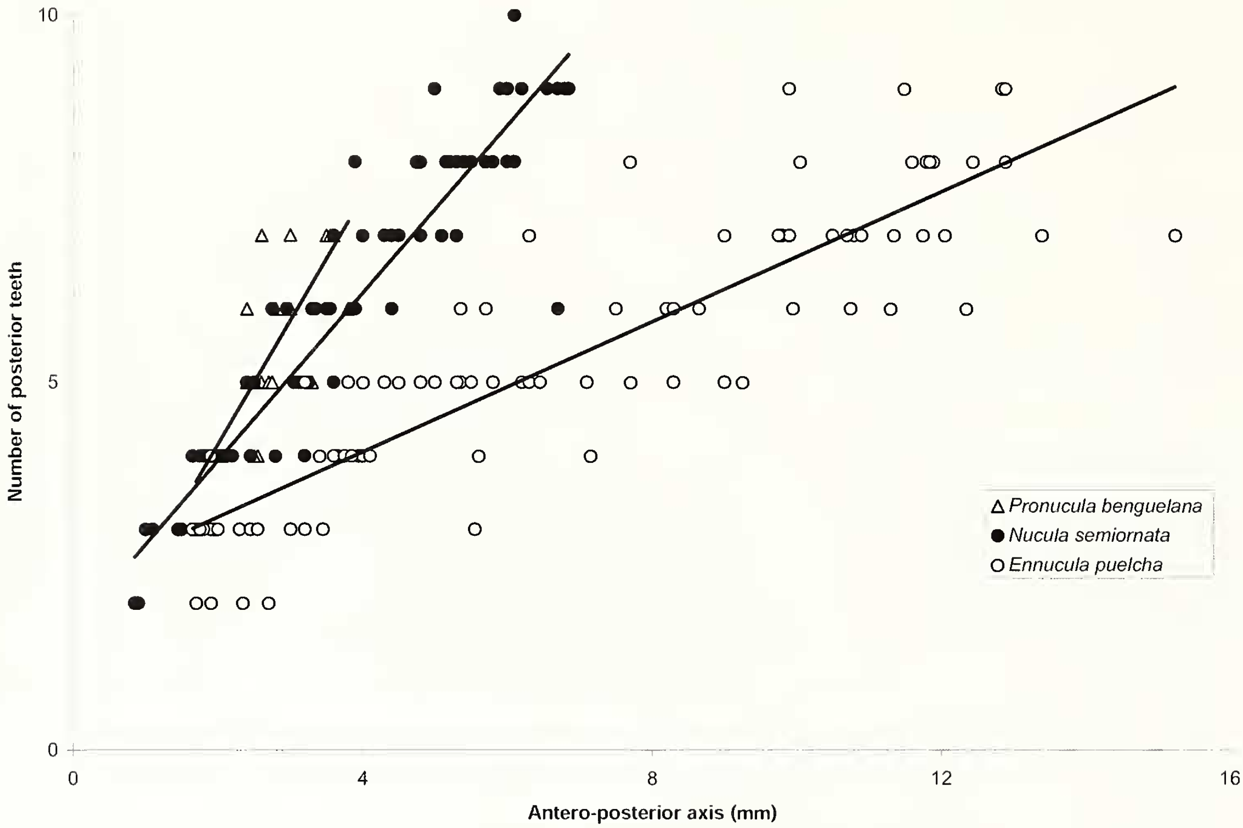


Figure 3. Relationship between: **A.** antero-posterior and **B.** dorso-ventral axes with the number of anterior teeth, showing the morphospaces overlap between *Pronucula benguelana* and *Ennucula puelcha*.



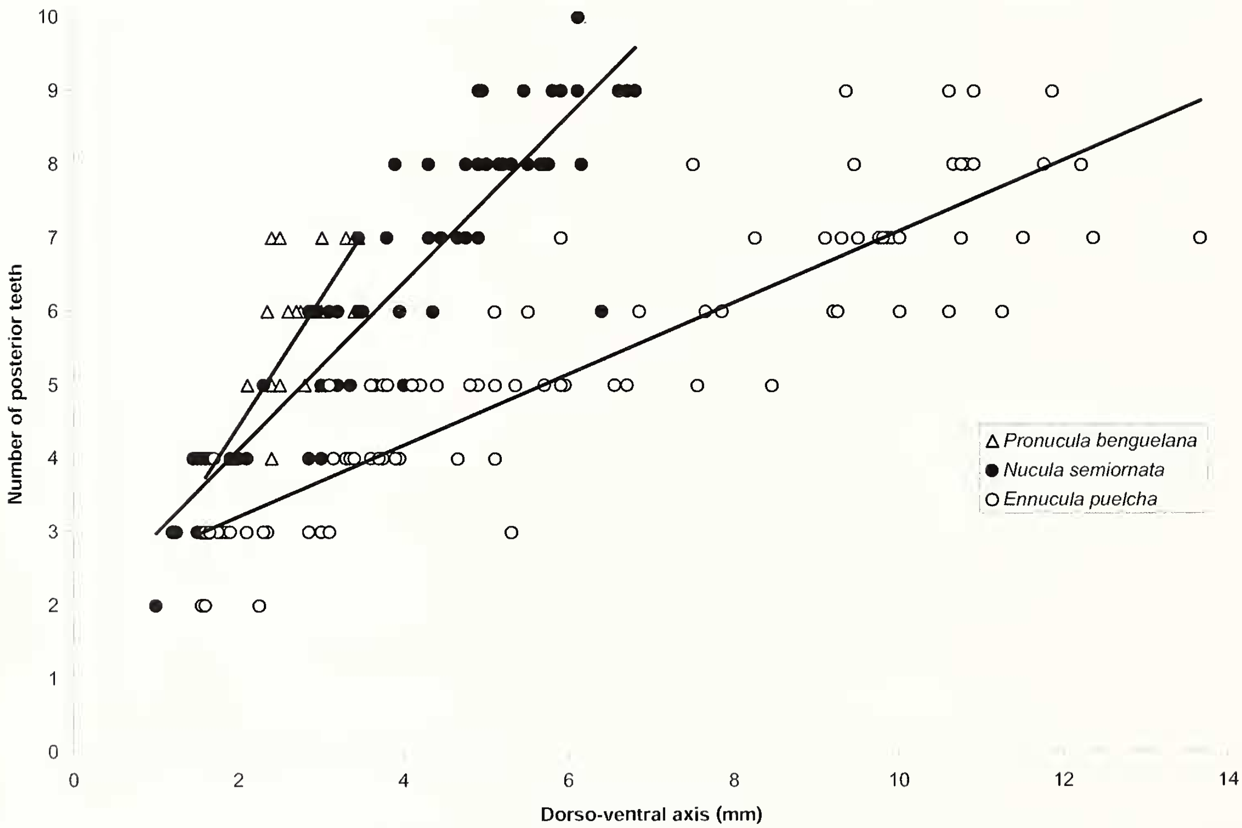


Figure 4. Relationship between: **A.** antero-posterior and **B.** dorso-ventral axes with the number of posterior teeth, showing the overlap of the morphospaces of *Pronucula benguelana* and *Nucula semiornata*.

RESULTS AND DISCUSSION

All the species studied exhibited a gradual increase of the number of anterior and posterior teeth during ontogeny. All results were statistically significant (Table 2), when we compared the importance of shell size with the number of anterior and posterior teeth. This statistical analysis confirmed the existence of a relationship between the two variables, size and number of teeth, and suggests that this relationship may be verified in other protobranch species. Furthermore, it confirmed the variation in the number of teeth for the same size class for each species studied. This attests to the inconsistency of this character when it is analyzed alone.

In addition, Figure 2 indicates a distinction among the genera *Adrana* and *Pronucula*, *Nucula*, and *Ennucula*, which becomes more evident when we compared the number of posterior teeth and the length of the dorsoventral axis. This result matches most accepted classifications that consider several characters (not only number of teeth) and allocate these three genera into two distinct groups (e.g. Allen and Hannah, 1986; Maxwell, 1988; Giribet and Wheeler, 2002; Giribet, 2008).

On the other hand, considering the Nuculidae, the morphospace of *Pronucula benguelana* overlapped with *E. puelcha* in the number of anterior teeth regressed on antero-posterior axis (Figure 3a) and on dorsoventral axis (Fig. 3b); and *P. benguelana* overlapped with *N. semiornata* in the number of posterior teeth regressed on antero-posterior axis (Figure 4a) and on dorso-ventral axis (Figure 4b). In both cases, these overlaps of the number of teeth (anterior or posterior) occurred up to about 4 mm in size, on each axis analyzed, for *P. benguelana*. Because this latter species is about 4 mm in size, this size limit in the overlap cannot be interpreted as a consequence of the number of specimens collected.

It is evident that the current taxonomy of Nuculidae presents confused generic definitions, not rare with a great correspondence of characters. Considering only the results presented herein, the overlaps of the morphospaces of *Pronucula* and *Nucula* are in agreement, and may reinforce the view of Bergmans (1978), who synonymized the two genera, or that of Allen and Hannah (1986), who proposed the allocation of *Pronucula*, at a subgeneric rank, to the genus *Nucula*. Along the same lines, the overlaps of the morphospaces of *Ennucula* and *Nucula* may reinforce the view of Schenck (1934) who placed *Ennucula* as a subgenus of *Nucula*. Nevertheless, because no other taxonomic features were analyzed in this study and, moreover, none of the species studied are type-species of *Pronucula*, *Nucula*, or *Ennucula*, this ratification of the opinions of above-mentioned authors may be premature.

CONCLUSION

These statistical analyses confirmed empirical observations of the relation between shell size and number of teeth in protobranch bivalves and attests to the inconsistency of the latter character when analyzed alone. For the taxa studied herein, the number of teeth on the hinge is an important taxonomic feature, but only when the size of the shell is also taken into account. Otherwise, taxonomic studies and descriptions based only on the number of teeth without providing any measures of the shell are not informative and might make it impossible to define whether one is dealing with several similar species or just one that shows intraspecific variation for the character number of hinge teeth.

The use of other characters in the taxonomy of the group is obviously important, but for the species studied here, at the family level, the distinction between *Adrana* (Nuculanidae) and *Pronucula*, *Nucula*, and *Ennucula* (Nuculidae) is in agreement with most accepted classifications. This attests the importance of number of teeth on the hinge related to the size of the shell for the distinction of these two families even when no other characters are considered. Nevertheless, for the nuculids, the differentiation of the distinct genera is unclear. The number of teeth on hinge and the size of the shell alone do not provided a good distinction among the three genera and the overlap of the morphospaces of these different taxa reinforces the demand for the use of more taxonomic characters and emphasizes the need for more comprehensive studies with these groups.

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